Marine Research

SCOTTISH HOME DEPARTMENT

Marine Research
1957 No. 3

The Food and Feeding Habits of Larval and Post-Larval Herring in the Northern North Sea

By R. N. BHATTACHARYYA, M.Sc., Ph.D. (Calcutta).

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The Food and Feeding Habits of Larval and Post-Larval Herring in the Northern North Sea

INTRODUCTION

Investigations into the food and feeding habits of the larval and post-larval herring have an important place in fisheries research. Works on this subject have previously been published by Lebour (1921, 1924) on the larval and post-larval herring of Plymouth area; Hardy (1924) on the young herring of the southern North Sea; and Ogilvie (1927) on the post-larval herring collected off the coast of Aberdeen. Marshall, Nicholls and Orr (1937) have described the food of young herring of the Clyde area, and Bowers and Williamson (1951) have investigated this problem in Manx waters. In addition to these there are a few scattered works on the food and feeding habits of larval and post-larval herring, with other observations such as those by Gross (1937), Kotthaus (1939), Schacht (1939) and Soleim (1942). References to some works that have been published since this paper was drafted in 1953 have been added to the text by Dr. J. H. Fraser.

The present work is the result of the examination of 2,521 specimens collected by the research vessels *Explorer*, *Scotia* and *Clupea* of the Scottish Home Department, during the month of April and from August to November, 1952. They were taken from various positions in the Moray Firth, Cromarty Firth and Fair Isle area of the North Sea.

ACKNOWLEDGEMENTS

My thanks are due to the Scottish Home Department for permission to work in the Marine Laboratory at Aberdeen, and for providing me with every facility in the laboratory during my investigation. I am greatly indebted to Dr. J. H. Fraser for suggesting this problem to me, for his valuable guidance and generous help throughout the work, and for kindly going through the manuscript and revising it. I also thank Mr. A. Saville and his assistants, who provided me with the herring larvae already sorted out from the plankton collections, and also Mr. R. Jones and Mr. T. Lovegrove for their valuable suggestions.

MATERIAL AND METHODS

The larval and post-larval herring were caught in the areas mentioned above by surface and sub-surface tow-netting with different types of plankton nets. They were preserved in 3% formalin in buffered sea water. A total of 137 specimens were examined from four April hauls, but none of them possessed a yolk sac. All those caught in August, totalling 147, were taken in a single haul and five of these possessed yolk sacs. In 24 hauls taken in September the largest number of larval and post-larval herrings were caught, a total of 1176, of which 31 had yolk sacs. In October, 19 hauls contained a total of 739 young herring, while nine hauls in November contained 322, but none of these had yolk sacs.

Almost all the August and September fish were examined, but sub-samples of 25 were taken from the October and November samples where the number of fish in the sample was over one hundred. Where the number of fish was smaller, all were examined. Each specimen was measured to the nearest millimetre and the measurements recorded, the data being subsequently classed into six size groups:—

1.	6 to 10 mm	4.	21 to 25 mm
2.	11 to 15 mm	5.	26 to 30 mm
3.	16 to 20 mm	6.	31 to 35 mm

Each was then transferred to a slide, the whole gut removed and slit open under a dissecting microscope with a pair of fine needles. The contents were spread over the slide, identified, and counted under the microscope.

Records of the food of each fish were kept separately. Broken or digested parts of nauplii, copepodite and adult copepods were identified as far as possible, but although the organisms were intact when undigested, generally only integuments were found after digestion had progressed. The gastropod and lamellibranch larvae, and the copepod eggs which had not been crushed, were broken by the needles and their condition observed in order to ascertain the degree of digestion. These results were also recorded individually. Full details are not reproduced in this paper, but may be consulted on application to the Marine Laboratory, Aberdeen.

Samples of the green patches found in the gut of larval and post-larval herring were examined under an oil-immersion lens and results were also recorded.

THE ALIMENTARY CANAL

The alimentary canal of larval and post-larval herring is a long, narrow transparent tube reaching from the mouth to the anus. A small constriction near the middle separates the anterior from the posterior part. The wall of the anterior part is thinner and narrower than that of the posterior. The posterior part is not only wider but is also more muscular. In fish from 6 to 35 mm in length, the anterior part of the gut remains a straight tube without any trace of diverticulum that could be called stomach or caecum, although thin patches of glands can be detected in its wall after staining with borax carmine. The posterior gut is much more glandular.

The larval and post-larval herring are very transparent, and the food taken by them is clearly seen with the naked eye, and is sometimes revealed by a swelling. While they seem to prefer food of a rounded shape, when they take copepods they succeed in swallowing most of them head first except *Oithona*, copepodite or adult, which is taken by the middle with the tail folded back as demonstrated by Ogilvie (1927). Lamellibranch larvae are swallowed by the smooth, broader (i.e. hinge) side, and *Limacina* is taken by the rounded surface.

Previous authors have already noticed that almost all food contents are found in the posterior part of the gut. Thus Ogilvie (1927) writes, "The food was practically all found in the intestine, and most of it in the hinder part. In only a very few (4) specimens, all over 40 mm, was anything found in the oesophagus, stomach or caecum, and in these very little." Marshall, Nicholls and Orr (1937) state, "The food was almost invariably in the intestine unless the fish had begun metamorphosis." In the present investigation 27 specimens out of 2,521 contained food in the anterior part of the gut and only 36 organisms were found there. When the fish are caught in the morning or just before evening—these are the two most usual feeding times—it might be expected that some would be found with food in the oesophagus or stomach, but even at these times only a very few such fish were seen. Food organisms swallowed by the herring thus appear to pass quickly through the anterior part of the gut, which takes part neither in digesting nor in storing the food. Perhaps the secretions allow the food organisms to pass through easily to the posterior part.

Not every organism was digested fully, and it was observed that some foods, including copepod eggs, dinoflagellates, diatoms and lamellibranch larvae, were accumulated at the terminal part of the gut ready for extrusion apparently without being digested at all. Copepods were digested very speedily. Limacina larvae were digested either after breaking the shells or by the gastric juice penetrating inside the shells, probably through the operculum. Thus in many cases it was noticed that the shells of Limacina were actually empty although they looked quite intact. The lamellibranch larvae with broken shells appear to be digested without difficulty, but those with whole shells appear to remain in the intestines long enough for the gastric juices to soften or break the shells.

THE FOOD OF LARVAL HERRING

It was found that some of the larval herring (i.e. yolk-sac stages) were feeding, and this has also been observed by almost all the previous authors. The North Sea herring larvae examined in the present investigation absorbed the yolk sac at a smaller size than those of the western English Channel. Lebour (1921) writes of the latter, "Those from 7 to 8 mm long nearly always possessed a yolk sac. From 8 to 9 mm the yolk sac was usually still present, and up to 10 mm it often persisted. Even at 12 mm remnants of yolk sac could sometimes still be recognised." A total of 36 larval herring with yolk sacs were found amongst the 2,521 specimens examined in the present investigation and their size ranged from 6 to 9 mm. They were all obtained in the August and September collections. Only one of these was 9 mm and it had but a remnant of yolk sac; most fish between 7 and 8 mm were without yolk sacs. None without yolk sac was found during April, October or November. This early absorption of the yolk sac was also observed by Hardy (1924), who states that in his North Sea samples it occasionally persists until a length of 11 mm is reached, whilst many have already lost it at a length of 6·5 mm.

The number of larvae examined with food in them was so small that it is not possible to come to any distinct conclusions, but it is only to be expected that the size of the food organisms themselves must play an important part in the choice of food. Amongst the 36 larval fish only four contained food, which consisted of *Coscinodiscus grani*, green patches and nauplii of *Pseudocalanus*, so that both vegetable and animal food appear to be taken, as Lebour and Hardy found. (See Appendix, Table I.)

FOOD OF POST-LARVAL HERRING

The young herring from the absorption of the yolk sac to the length of 35 mm have been considered as post-larval. No fish of less than 35 mm was seen to be at the metamorphosing stage. The food of these post-larval herring, although including quite a wide range, usually consisted of the following:

(a) Centric diatoms
(b) Green patches
(c) *Ptychocylis minor* (Tintinnoidea)
(d) *Peridinium depressum*
(e) Copepod eggs
(f) Nauplii copepodites and adults of copepods
(g) Larvae of lamellibranchs
(h) Larvae of *Limacina retroversa*

Other organisms were of such rare occurrence that their importance as food was negligible. They were:

Gyrosigma sp. (diatom)—one only;
Larvae of *Balanus*—one only;
Monoculoides carinatus (amphipod)—two only;
Spionid larvae (polychaete)—two only

(See Appendix, Table II.)

Larval molluscs and copepods, including eggs, formed the staple food of the specimens from the hauls in August, September, October and November. April specimens showed no trace of mollusc larvae, and the fish were found to have fed exclusively on copepods of all stages, including eggs. Copepod eggs were found in April, September, October and November; they were not present in August while in November they occurred in reduced numbers. Protozoan food—*Ptychocylis minor*—was taken by post-larval herring in September and October. Relatively few were found in September but in October they occurred in quantity, and indeed exceeded any other organism in numerical abundance, although not in bulk. A few dinoflagellates—*Peridinium depressum*—were found, but only in November, and then more often in the smaller larvae. Green patches were found in all sizes of fish.

VEGETABLE DIET AND THE GREEN PATCH

It had previously been thought that larval herring fed entirely on a vegetable diet and changed to a completely carnivorous diet as soon as they became post-larvae. Lebour (1921) found no plant food in those over 12 mm, i.e. after the disappearance of the yolk sac. The present work suggests, however, that the change is much more gradual; one 8 mm larva had eaten a *Pseudocalanus* nauplius while post-larval fish up to 17 mm contained a few centric diatoms (*Coscinodiscus concinnus*, *C. radiatus*, *C. grani*, *C. lineatus* and *C. excentricus*) and one species of *Gyrosigma*, although the importance of these diatoms in comparison with other food, such as copepods and molluscs, seemed almost negligible. These diatoms were taken by the fish in August and September, but were not seen in collections from April, October or November.

Qasim (1955) found experimentally that the larvae of some shore fishes would take phytoplankton, but this alone contributed little to survival, hardly more than no food at all. When phytoplankton was taken with nauplii the results differed little from when nauplii alone were taken.

The green substance which was often found in the gut occurred as patches of two kinds. Such patches have been noticed and described by previous authors as "green remains," "green food matter," "green mass," etc. and their origin has apparently only been assumed. Thus Lebour (1921) says, "The green remains are probably the remains of unicellular plants." Hardy (1924) considers these ". . . unidentifiable green food matters" to be "probably flagellates." Marshall, Nicholls and Orr (1937) write, "A greenish mush, possibly the remains of diatoms or flagellates." Bowers and Williamson (1951) state, "Flagellates almost certainly come in this category and are thought to be the main source of the 'green remains'." These opinions indicate that though these green patches were considered to form an important part of the food of larval and post-larval herring their precise origin has not been very clear.

Dr. J. H. Fraser analysed samples of these green patches for me under an oil-immersion lens; I quote here his report on one of these types, "A matrix of slime with solid bodies embedded in it; fully 90% of these are minute fragments of transparent grains believed to be silica, many of them so small that brownian movement is active. A few cocoliths are present, also the chloroplasts of what may have been μ— flagellates and a number of round blue-green spores 4μ in diameter. There is no sign of crustacean fragments or any broken shells of diatoms or dinoflagellates." This type of green patch was never observed to be adhering to any other of the food organisms within the gut. It was observed, accompanied by no other food, in the gut of larval and early post-larval fish between 6 and 12 mm, but occurred with other food in fish up to 13·5 mm. It was not found in November when the specimens examined were all over 12 mm, nor in April.

Another type of green patch was often mixed with the broken parts of copepods and molluscs, and was found in all sizes of fish. One of these was also analysed for me by Dr. Fraser with the following result, "This green patch appears to be a remnant of a faecal pellet of either copepod or molluscan origin. It seems to have been unaffected by the digestive juices of the larval herring, presumably because of some protective covering or matrix secreted by the animal concerned. Differential staining shows the presence of protein but there does not seem to be any trace of cellulose left in it." Since writing this Forster (1953) has shown that the membrane surrounding the faecal pellets of various shrimps and prawns is of a chitinous nature. Shelbourne (1953) found that certain pellets in plaice post-larvae were the faeces of Oikopleura which had been eaten by the fish.

Table II records only the green patches of the former type which, although not all examined in detail, are believed to be the conglomeration of various algae possibly deliberately taken by the fish. The latter type was excluded as it is considered that it would probably not be utilised as food, whether eaten deliberately, or merely left in the gut after the digestion of the animal producing it.

THE IMPORTANCE OF MOLLUSCAN LARVAE AS FOOD

Larvae of various species of lamellibranchs and the gastropod *Limacina retroversa* formed an important part of the food of post-larval herring during autumn. About 35 types of lamellibranch larvae were recognised including the veliger larvae which could not be specifically identified: identifications of the

shelled larvae were made according to Rees (1950). Veliger larvae of lamellibranchs were an important part of the autumn diet and were increasingly abundant from August to November. Lamellibranch post-larvae (i.e. excluding the veligers), were also found in large numbers, the most common species being *Saxicava arctica*, *Musculus marmoratus*, *Spisula subtruncata*, *Tellina pygmaea* and *Cardium sp.* Although lamellibranch larvae were found in all the four months of autumn, their variety in species, number and occurrence increased in October and November. The largest number seen in any one specimen was 21 in a fish of 29 mm in October.

Larvae of only one gastropod—*Limacina retroversa*—were recorded. They were found throughout September, October and November, and were certainly the dominant food during October. None was seen in either April or August. In September 42 *Limacina* larvae were taken in 345 fish; in October 1582 were found in 342 fish; and in November 333 were found in 124 fish. The largest individual number of *Limacina* was 62 in a 14 mm fish in October and no other organism except the tintinnid *Ptychocylis minor* even numerically exceeded this figure. Numbers of *Limacina* between 20 and 25 were common in both October and November.

THE IMPORTANCE OF THE COPEPOD DIET

Nauplii, copepodites and adult forms of copepods were detected in the food of almost all the post-larval herring from both spring and autumn hauls. Perhaps copepods and their various stages are the only food which could be taken readily from the plankton throughout all the five months investigated. The copepods identified here belonged to the following genera: *Calanus*, *Paracalanus*, *Microcalanus*, *Pseudocalanus*, *Metridia*, *Acartia*, *Centropages*, *Temora*, *Oithona*, *Microsetella*, *Halithalestris* and *Euterpina*.

Not all of the development stages of all these copepods were found. Nauplii only were seen of *Paracalanus*, *Microcalanus*, and *Metridia*; nauplii and copepodites but no adults of *Calanus*, *Centropages*, *Temora* and *Acartia*; all stages of *Microsetella norvegica*, *Pseudocalanus* and *Oithona*, including egg sacs of *Oithona*, both free and attached. *Microsetella rosea*, *Halithalestris* and *Euterpina* were rare and found as adults only. The nauplii were identified from Ogilvie (1956) which I was privileged to see in manuscript.

The absence of the adult stages of the larger copepods can probably be simply explained by their size, and the other discrepancies are probably due to chance sampling of the fish and the chance nature of their feeding. Where it was not possible to identify the broken bits of copepods, nauplii or copepodites, they were recorded under the general term "unidentified broken copepods."

The months in which the various stages of different species of copepods were obtained and their relative importance as food are shown in Table II. It should be noted that *Calanus* was rarely taken by these post-larval fish, and then only in its young stages, whereas *Pseudocalanus* was of major importance. Although nauplii of *Pseudocalanus* were taken by fish of all sizes the proportion of nauplii to older stages became reduced as the season advanced. This can be explained partly by the lesser proportion of nauplii in the sea in late autumn and partly by the fish of increased size having a preference for larger items of food. Only fish greater than 15 mm contained copepodites or adults. *Paracalanus* showed similar features but was taken in smaller numbers. The other calanoid copepods taken as food were too few to show clearly the principle on which food was taken. *Oithona*—chiefly *O. similis*—was also an important item of diet and was in fact numerically the most abundant species of copepod taken. With *Microsetella* it was, like the calanoids, dominant in October and November. These two species have very small nauplii which may account for their relative scarcity in the food. Copepod eggs were often taken, many of which were *Oithona*; these may have been ingested as egg sacs attached to adult females, and indeed whole egg sacs were seen on several occasions.

THE CHOICE OF FOOD

It would appear that the feeding of larval, and especially of post-larval herring, primarily depends on the availability of the planktonic organisms in the surrounding water where they live. Larvae of molluscs, which can be considered as one of the main sources of food, were eaten in large numbers in

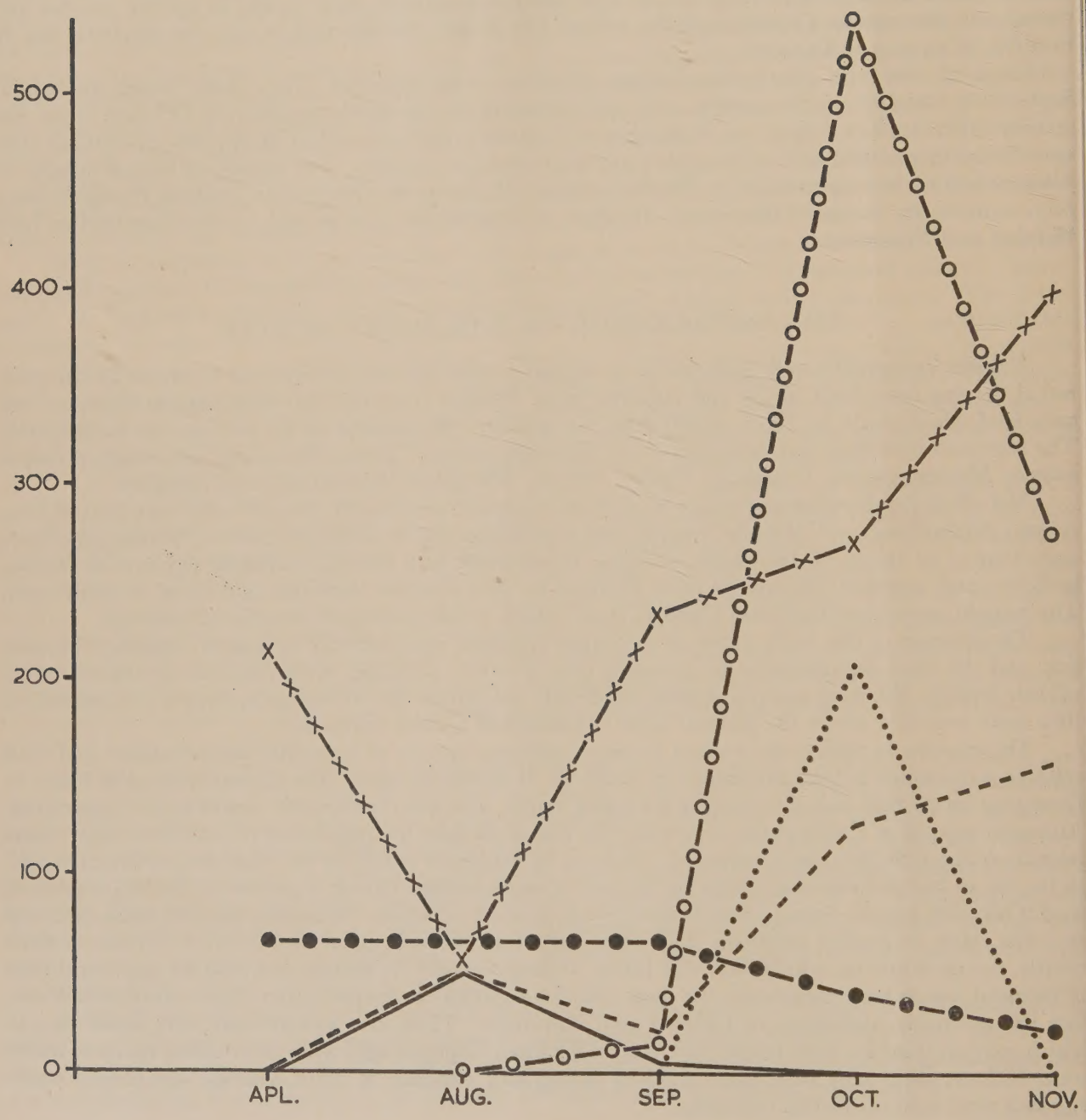

Fig. 1 The average number of organisms per 100 fish in different months:

–·–·–	copepod eggs	------	Lamellibranch larvae
–x–x–	all other stages of copepods	·····	*Ptychocylis minor*
–o–o–	*Limacina retroversa*	——	diatoms

the autumn when the species concerned are most plentiful in the sea (Rees, 1951); the only notable exception was that the larvae of *Ensis*, which is regarded as a spring spawner, were identified from fish taken in October and November. In spring and early autumn, when the nauplius stages of copepods were plentifully available in the plankton, they were quite numerous in the food, but in November when there would normally be fewer nauplii, their numbers in the gut also decreased and the numbers of adults and copepodites proportionately increased. On the other hand, although the plankton from the same hauls as the fish samples has not been examined in detail, it would seem that many other planktonic forms must have been available and not taken by the fish. Fleury (1953) noted that *Euterpina* was always present in her samples of pilchard stomachs even when it was not found in the plankton collections. In view of this the single record of *Euterpina* in the October samples is possibly of interest as this copepod is so very rarely found in the plankton of the northern North Sea. Although the food or relative proportions of the food are primarily dependent on availability there is thus probably also a selective process in the feeding. The relative importance of the various food constituents is shown in Fig. 1.

THE LIGHT FACTOR IN THE PROCESS OF FEEDING

Light appears to be a most important factor in the process of feeding of larval and post-larval herring. Thus, in his investigations on the feeding behaviour of young herring by artificial feeding, Schacht (1939) observes, "It is therefore very useful if the light falls directly on the rearing basin from above so that the prey stand out better against the surface of the water. Where glass aquaria were used with the lighting only from one side, on account of the positive phototaxis the herring larvae remain at the sunlit side of the aquariaum and refused all food that was offered to them"—(Translated from the German). In 1942 Soleim states, "It was furthermore found that light is of great importance for the active feeding of the larvae." Woodhead (1955) showed that light was also a factor in effecting vertical migration, and that in the light they will swim longer in a horizontal direction. This would increase their chances of finding food. In the present work it was found that a great number of larvae and post-larvae, taken during the night and early morning, were quite empty of food, whilst samples taken in daylight contained food. In September and October, when a large number of specimens were examined, it was observed that the percentage containing food was always highest in the samples collected during the morning or before sunset. After sunset the proportion of fish containing food declined sharply. A rise in the percentage of feeding fish just before sunset (Fig. 2) perhaps can be explained by greater activity in the young fish, as a result of changing light intensity.

Freshly digested food was found in the gut throughout the day, and food in the oesophagus, which can be regarded as evidence of being very recently ingested, also occurred most frequently during the day. The food found in the fish caught in the morning was mostly fresh and undigested, whereas about half the fish were found to have partly digested food in hauls taken from mid-day up to just before sunset. About an hour after sunset an increased proportion of the food was again found to be fresh and undigested, which confirms increased feeding activity at about sunset. As the hours of darkness progressed the condition of food was found to be more and more broken and digested, and by about midnight digestion was almost always complete. From 1 a.m. to the time of sunrise, all the fish remained entirely empty except for a stray integument of a copepod, or a shell of lamellibranch. This pattern of feeding followed the variation of the time of sunrise and sunset from month to month.

Although not many April specimens were obtained, a rise was observed in the percentage containing food in the afternoon followed by a sharp fall after darkness (Fig. 2). No range of times is available from the August sampling. In September the percentage of feeding was observed frequently during the 24 hours, and the rise in percentage of feeding in the morning and evening was obvious, followed by a marked drop during darkness. In October the high rate of feeding in the morning was again noted, but there was also a small rise immediately after sunset. This small rise may not be significant but could perhaps be explained as the evening in question had a prolonged twilight and full moon, so that it might have been possible for the herring to see their food for a time even after sunset. The November sampling did not cover the whole period between dawn and sunset, but the rise in percentage containing food

between these two times is shown. The continued rise after sunset may be due to the greater proportion of less easily digestible food such as lamellibranchs taken at this time of the year, but one must not stress this possibility in view of the small number of samples.

It would appear from these observations that the larval and post-larval herring started feeding with the sunrise and went on taking and digesting food throughout the day, but with an increased intensity at about sunset.

Qasim (1955) found similar effects of light and darkness on the feeding of blennies and other shore fish in experiments made in tanks where the light and dark periods could be controlled. He found that feeding on nauplii stopped in darkness and that there was a greater feeding activity when the light was put on after a dark period than when the light had been continuous. A further interesting feature

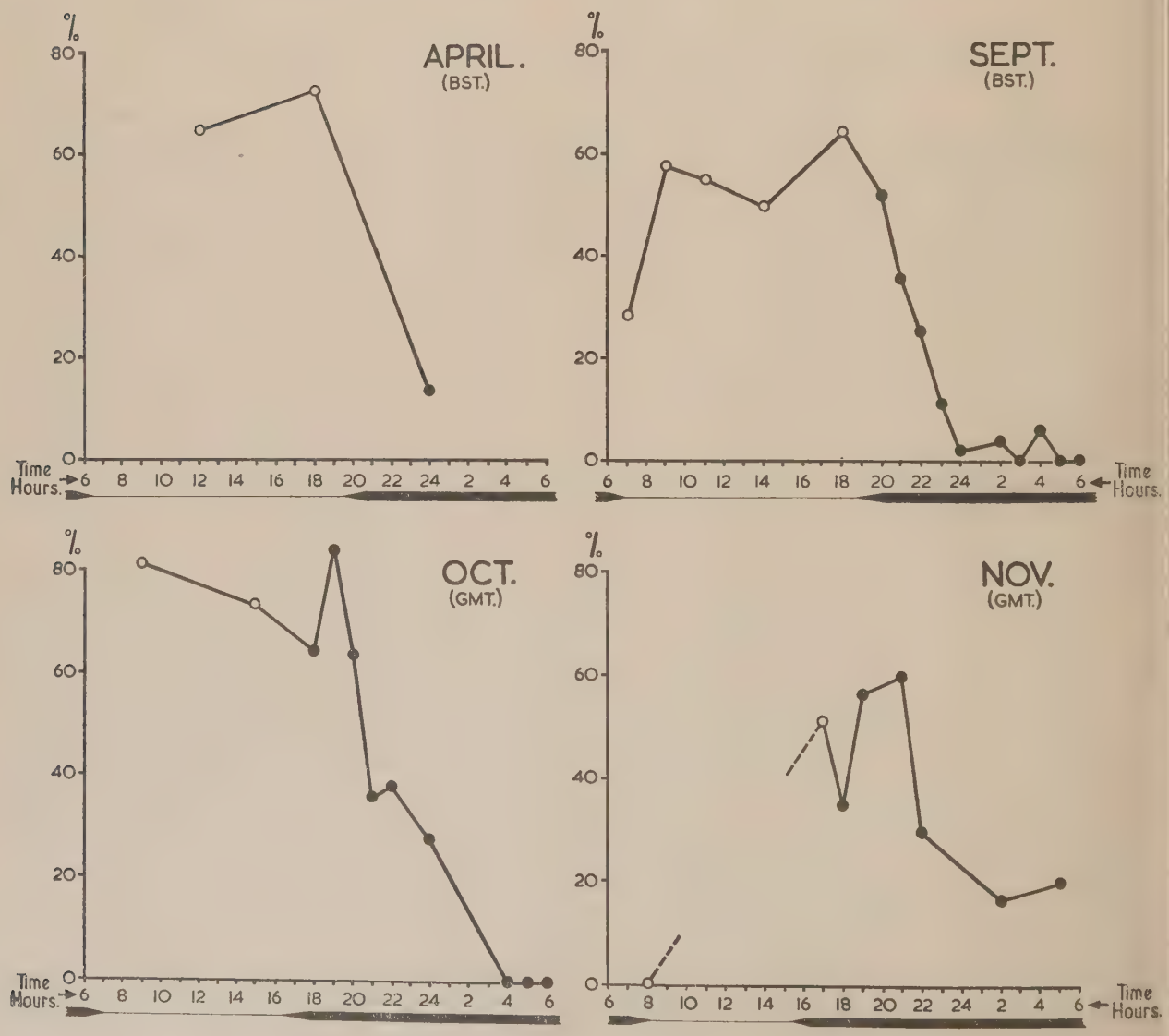

Fig. 2 Percentage of post-larvae containing food at different hours of the day. Hours between sunset and sunrise are indicated by a dark band, and the tapering ends of this show the range through the month.

was that survival was better when there were alternating periods of light and dark than in continuous light with food available at all times, thus suggesting a need for rest or even 'sleep'. Shelbourne (1953) also noted a marked diurnal feeding in the post-larval stages of plaice, with a rise in activity both before and after noon, with a quiescent period during darkness. He confirmed his results with tank experiments.

When it became obvious that the larval and post-larval herring did not usually take food after darkness, an attempt was made to find out the rate of digestion of the different types of food. The chief items were the copepods (including nauplii, copepodites and adults), copepod eggs, lamellibranch larvae and larvae of *Limacina retroversa*. The progress of digestion of each individual organism from sunset to midnight was investigated; the results are shown in Appendix, Table III.

As feeding has taken place no longer than one hour after sunset, except perhaps in November, the degree of digestion at different times during the night gives an indication of the minimum rate of digestion, and as freshly ingested food was frequently seen just before sunset, or immediately after, the figures may be fairly representative.

As no specimen taking copepod food was caught after sunset in April or August, observations on the rate of digestion of this type of food were confined to September, October and November. It was noticed that in these three months copepods were digested quite soon after sunset, i.e. over 90 per cent within an hour, as against an average of about 40 per cent. during daylight hours. Copepod eggs, which had been one of the chief diets of the fish in September and October, were not digested so quickly, probably owing to their tough shell, and in September it was at least 4 hours after sunset before they were thoroughly digested. In October the copepod eggs were taken with a large number of lamellibranch larvae, and in such individuals the limited amount of digestive juice, and perhaps the large proportion of alkaline shell, may have been responsible for copepod eggs remaining undigested for about an hour longer than in September. There is no adequate information for November.

Lamellibranch larvae were taken abundantly in October and November, and it was very easy to record the rate of their digestion in these two months. It was observed that they took longer to digest than other types of food presumably due to their hard shells. They generally took four to six hours to be completely digested and were often found intact even to quite a late hour after midnight. Those lamellibranchs, which broke easily, such as *Monia*, *Tellina*, etc., were digested more quickly than the hard-shelled types like *Saxicava* or *Cardium*.

The rate of digestion of larvae of *Limacina retroversa* was also observed in October and November. The presence of only the opercula of Limacina was regarded as evidence of complete digestion. Digestion appears to vary according to the ease with which the juice first penetrates, and may take between two and six hours. Though quite a large number of them were found to be digested soon after sunset, they were not all digested until much later.

PARASITES

There was a very small degree of metazoan parasitism, only 12 parasites, all cestodes, were found in 2521 fish. They were found in the intestines of fish taken in October and November only and were not found in fish less than 13 mm in length.

THE PRESENT WORK IN COMPARISON WITH PREVIOUS WORKS

Hardy (1929), Lebour (1921, 1924), Marshall, Nicholls and Orr (1937) all emphasised the importance of vegetable food in the larval herring, though Hardy says that there is no phase in which vegetable food alone is taken, and Lebour (1921) places larval gastropods first on the list of food organisms and includes also lamellibranch larvae, nauplii and eggs. Marshall, Nicholls and Orr, referring also to the previous authors, write, "It is well known that herring larvae feed first on the diatoms and unicellular organisms." The results of the present work agree with Lebour (1921), Hardy (1924) and with Bowers and Williamson (1951), who have shown the importance of both animal and vegetable diet, and

with Soleim (1942), who writes, "Contrary to earlier suppositions it was found that a vegetarian diet alon was unable to keep the larvae alive in early life." This view has also been supported by the observation of Kotthaus (1939) who emphasised the presence of copepod nauplii as well as a green structureless mass

The present investigations differed considerably from those of Ogilvie (1927), and Marshall (*et al*) (1937) on the food of post-larval herring. Lebour mentions the importance of gastropod larvae as food o larval herring and also of the smaller post-larval fish. Ogilvie, and Marshall (*et al*), recorded no mollus larvae in their specimens, and Hardy writes, "In comparing the results obtained with those of Lebou it will be seen that they agree except that larval gastropods and lamellibranchs are not found to be a important part of the diet; for the Plymouth area she places the larval gastropods first and larval lamell branchs third in importance in the food of youngest herrings, whereas here one has only found the forme in one specimen and the latter in four—all from one sample." This difference may be due to the time o year of collection, and it is probable that Hardy's samples were taken in mid-winter when these larva would not have been so abundant. The present work shows that lamellibranch and gastropod larva can play a very important part in the diet of young herring of all stages. The importance of mollus larvae as the food of post-larval herring has recently been stressed by Bowers and Williamson (1951) working on specimens from Manx waters. Although they did not record mollusc larvae from any post larval fish in September (in the present work mollusc larvae were found in fish collected in August September, October and November), they show an almost similar result, recording these larvae a occurring in considerable numbers especially in October and November. They also observe, "Thus lamellibranch larvae showed a maximum in October and gastropod larvae in November," but in th present work it is noticed that gastropods and veligers of lamellibranchs occurred more frequently an in greater numbers in October than in November, and shelled lamellibranchs were most abundant i November.

All previous observations record that *Pseudocalanus* is dominant in the diet of fish between 15 an 25 mm, the importance of other copepods being much less. *Oithona* has been recorded as an importan food of herring below 15 mm by Bowers and Williamson but not by previous authors. The prese observations on North Sea specimens show that *Oithona* was dominant numerically in the diet of pos larval herring. It was dominant in all those examined and exceeded *Pseudocalanus*, which was second, i volume as well as in number.

It is, of course, appreciated that the present limited work is based on the results from a few montl of one year only, and there may well be variations from year to year and from place to place, partl dependent on the annual and spatial variations in the availability of the organisms in the plankton, an partly on variations in selective feeding.

As a reason for the large percentage of stomachs which were found empty, Lebour writes, "A probabl reason for this apparent absence of food in the transparent stages is that the food must be very quickl digested on account of its being so conspicuous; thus it is probably taken only at long intervals or rapidl got rid of." Hardy says that the young herring are extremely sensitive, so at the time of catching, "Th young herring at once started to get rid of their food from the intestine and could be seen rapidly shootin out the remaining faeces or probably part-digested food. Thus the 'reduction of ballast' in the face o danger is, the writer ventures to believe, a more likely explanation than Dr. Lebour's of the fact tha so many of the post-larval herring examined are empty."

As neither Lebour nor Hardy have recorded the state of daylight or the times of capture, it is n possible to reconsider their results in the terms of the argument now suggested. Neither of their reason appear in itself to be quite satisfactory and it may have been that their empty specimens were large taken at night. It is shown here that digestion may take several hours; it is difficult to conceive that th 'reduction of ballast' theory could be applied to only a proportion of fish caught and preserved in th same way, and it seems unlikely that it should occur more in fish caught at night than in daylight.

SUMMARY

The stomachs and intestines of 2521 larval and post-larval herring taken in the Moray Firth, Cromarty and Fair Isle areas were examined from collections made in April, August, September, October and November, 1952. It was found that 887 of these contained food organisms.

Only 36 of these were larval (yolk-sac stages) and of these only four contained food. This consisted of green patches, centric diatoms, and a copepod nauplius.

The anterior part of the gut is used mainly as a passage, all storage and digestion taking place in the posterior gut.

The food of post-larval herring included copepod eggs, adult copepods with nauplii and copepodites, lamellibranch larvae, gastropod larvae, centric diatoms, tintinnids and dinoflagellates.

Copepod eggs were found in all the months except August, and were most abundant in September and October.

Nauplii, copepodites and adults of copepods were taken in all five months. *Oithona* and *Pseudocalanus* were numerically dominant.

Lamellibranch larvae and gastropod larvae were taken abundantly in August, September, October and November. They were found to be present in specially large numbers in October and November.

Though of only little importance, diatoms were found to have been eaten in August and September, tintinnids in September and October, and dinoflagellates in November.

It is shown that the light factor plays a very important part in the feeding of young herring, and that larval and post-larval herring feed very little after darkness and start feeding with daybreak.

An attempt has been made to estimate the rate of digestion of copepods, copepod eggs, lamellibranch and gastropod larvae.

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APPENDIX

TABLE I

The Food of Larval Herring

Date of Capture	Time of Capture	Length in mm.	No. Examined	No. Feeding	Food
23.8.52	22.55 hrs.	7	4	1	Green Patch
		8	1	0	—
7.9.52	18.15 hrs.	6	1	0	—
		6·5	2	0	—
		7	2	0	—
		7·5	2	1	Green Patch
		8	1	1	Green Patch, nauplius of *Pseudocalanus*
8.9.52	20.13 hrs.	7	1	0	—
	23.48 „	7	5	0	—
		7·5	2	0	—
		8	1	0	—
9.9.52	00.53 hrs.	6	2	0	—
		6·5	2	0	—
		7	3	0	—
		7·5	1	0	—
	21.18 hrs.	6	1	0	—
10.9.52	11.39 hrs.	6·5	1	1	*Coscinodiscus grani*
11.9.52	11.44 hrs.	7	1	0	—
		7·5	1	0	—
		8	1	0	—
		9	1	0	—
	Total	—	36	4	

TABLE II.—See overleaf.

TABLE III

The percentage of digestion of four types of food in the hours of darkness

	Time	Hours After Sunset	Copepods	Copepod Eggs	Lamellibranch Larvae	*Limacina*
Sept.	20.00	¾	95	10		
	21.00	1¾	96	30		
	22.00	2¾	96	30		
	23.00	3¾	100	100		
	24.00	4¾	00 1	100		
	02.00	6¾	100	100		
Oct.	19.00	½	100	1	15	60
	20.00	1½	98	30	2	50
	21.00	2½	100	10	33	86
	22.00	3½	100	?	50	80
	24.00	5½	100	67	78	95
Nov.	18.00	½	90		15	94
	19.00	1½	94		30	70
	21.00	3½	100		100	78
	22.00	4½	100		100	100
	02.00	6½	100		100	100

	April, 1952												August, 1952												
Length in mm.	7	11	12	13	14	15	16	17	18	19	20	Total	7 7·5	8 8·5	9	10	11	12 12·5	13	14	15	16	17	18	19
No. Examined	1	11	5	17	23	23	18	18	14	3	4	137	13	43	41	23	3	7	2	2	1	5	4	1	1
No. Feeding	1	9	0	8	8	10	5	8	6	0	2	57	2	11	14	6	1	1	0	0	0	1	0	0	0
Coscinodiscus concinnus														1											
C. radiatus														1	2										
C. excentricus														1		4		1							
C. grani																									
C. lineatus														2	1	3									
Gyrosigma sp.																									
Green patches													2	8	8	8									
Peridinium depressum																									
Ptychocylis minor																									
Spionid larvae of polychaetes									1			1													
Veliger larvae of lamellibranchs														5	6		1								
Mactrid larvae																									
Larvae of *Glycymeris glycymeris*																									
,, ,, *Musculus marmoratus*																									
,, ,, *Mactra corallina*																									
,, ,, *Limopsis sp.*																									
,, ,, *Montacuta ferruginosa*															1										
,, ,, *Spisula elliptica*																									
,, ,, *S. subtruncata*																									
,, ,, *Monia squama*																									
,, ,, *Heteranomia squamula*																									
,, ,, *Anomia ephippium*																									
,, ,, *Venus sp.1*																									
,, ,, *Venus sp.2*																									
,, ,, *Modiolus modiolus*																									
,, ,, *Gari fervensis*																									
,, ,, *Astarta sp.*																									
,, ,, *Adula simpsoni*																									
,, ,, *Tellina pygmaea*																									
,, ,, *T. fabula*																									
,, ,, *Ensis siliqua*																									
,, ,, *Lima sp.*																									
,, ,, *Hiatella arctica*																									
,, ,, *Cardium sp.*																									
,, ,, *Cardium ovale*																									
,, ,, *Teredo sp.*																									
,, ,, *Cultellus pellucidus*																									
,, ,, *Lepton squamosum*																									
,, ,, *Abra prismatica*																									
,, ,, *Mya truncata*																									
,, ,, *Aloidis gibba*																									
,, ,, *Hiatella gallicana*																									
,, ,, *Mytilus edulis*																									
,, ,, *Montacuta substriata*																									
,, ,, *Zirfaea sp.*																									
Unidentified lamellibranch larvae															3										
Lamellibranch eggs																									
Gastropod eggs																									
Limacina retroversa																									
Copepod eggs	1	10		1	3	10		3			4	32													
Nauplius of *Calanus*																									
Copepodite of *Calanus*																									
Nauplius of *Pseudocalanus*		4		3	3	1	5					16					1								
Copepodite of ,,																									
Adult ,,																									
Nauplius of *Paracalanus*		11		5		2	1	1	3			23													
,, ,, *Microcalanus*		1		4		1						6													
,, ,, *Metridia*				1	1	1	1					4													
,, ,, *Acartia*				1	1	1		2				5													
Copepodite of *Acartia*																									
Nauplius of *Centropages*																									
Copepodite of ,,																									
Nauplius of *Temora*																									
Copepodite of *Temora*																									
Nauplius of *Oithona*					1	4	1					6													
Copepodite of *Oithona*					1	3		3	1			8													
Adult of ,,					1	2		3	2			8													
Eggs of ,,									6			6													
Nauplius of *Microsetella norvegica*				1				1				2													
Copepodite of ,, ,,				1	1	1						3													
Adult ,, ,,				1								1													
,, *M. rosea*																									
,, *Euterpina acutifrons*																									
,, *Halithalestris sp.*																									
Unidentified broken Copepods				2			4	4	4		2	16		3	1							1			
Amphipodite of *Monoculodes carinatus*																									
Nauplius of *Balanus*																									
Miscellaneous																									

	September, 1952																							
	6 6·5	7 7·5	8 8·5	9 9·5	10 10·5	11 11·5	12 12·5	13 13·5	14 14·5	15 15·5	16 16·5	17 17·5	18	19	20	21	22	23	24	25	28	29	30	Total
nined	9	31	70	168	253	152	143	82	52	58	28	25	22	27	30	5	6	6	1	4	1	1	2	1176
ing	1	3	16	43	68	65	63	24	16	10	8	5	8	8	4	0	1	2	0	0	0	0	0	345
nodiscus concinnus												1												1
diatus				1	3																			4
centricus				1	1	3	1																	6
ani	1			1			1	1																4
neatus																								
sigma sp.																								
n patches			9	14	18	6		1																48
nium depressum																								
ocyhis minor						2		1																3
nid larvae of polychaetes ..																								
ger larvae of lamellibranchs ..			8	3	11	8	1	1		1														33
trid larvae							1																	1
ae of *Glycymeris glycymeris* ..																								
,, *Musculus marmoratus* ..																								
,, *Mactra corallina*								4																4
,, *Limopsis sp.*																								
,, *Montacuta ferruginosa* ..								1																
,, *Spisula elliptica*						1	1																	1
,, *S. subtruncata*						2	1																	2
,, *Monia squama*				2	7	1	5																	3
																								15
,, *Heteranomia squamula* ..																								
,, *Anomia ephippium*																								
,, *Venus sp.1*																								
,, *Venus sp.2*								1																1
,, *Modiolus modiolus* ..					1																			1
,, *Gari fervensis*																								
,, *Astarta sp.*																								
,, *Adula simpsoni*																								
,, *Tellina pygmaea*																								
,, *T. fabula*																								
,, *Ensis siliqua*																								
,, *Lima sp.*																								
,, *Hiatella arctica*																								
,, *Cardium sp.*																								
,, *Cardium ovale*																								
,, *Teredo sp.*																								
,, *Cultellus pellucidus*																								
,, *Lepton squamosum*																								
,, *Abra prismatica*																								
,, *Mya truncata*																								
,, *Aloidis gibba*																								
,, *Hiatella gallicana*																								
,, *Mytilus edulis*																								
,, *Montacuta substriata* ..																								
,, *Zirfaea sp.*																								
dentified lamellibranch larvae ..			1		1		1																	3
ellibranch eggs																								
ropod eggs				3	1	2	2	3	1		1		1											14
cina retroversa			2	4	3	15	5	4	5	1	3													42
epod eggs		1	6	24	42	36	29	13	15	2	6	13	8	7										192
plius of *Calanus*						3	6			1	1													11
epodite of *Calanus*					1		1	1				1	1											5
plius of *Pseudocalanus*		1	3	9	13	44	33	9	10	5	3	6	3	3	1									143
epodite of ,, ...		1		2	1	8	3	4	2	10	3	1	5					1						41
lt ,, ...								2									1							3
plius of *Paracalanus*			1	5	17	13	11	3	4	5	4		4	2										59
,, ,, *Microcalanus*				1					1															2
,, ,, *Metridia*		1			1	3	1		1															7
,, ,, *Acartia*				1		4	5		2	1			2											15
epodite of *Acartia*						1	1		1			1	1											5
plius of *Centropages*				1	1	7		1			1													11
epodite of ,, ...					2	2			1															5
plius of *Temora*		1		1	4	8	12	4	1				2		1									34
epodite of *Temora*					3	9	13	5	2	2	2	3	1	1	1									42
plius of *Oithona*						2																		2
epodite of *Oithona*				3		8	9	3		1	7	2	4	9	11									57
lt of ,, ...					1	7	27	12	6		2		1	7	3									66
of ,, ...				2		30	20	20			2		16	2	3									95
olius of *Microsetella norvegica* ..																								
podite of ,, ,, ..																								
lt ,, ,, ..							1																	1
M. rosea																								
Euterpina acutifrons																								
Halithalestris sp.																								
dentified broken Copepods ..			3	16	14	26	15	5	3	6	2			1										91
hipodite of *Monoculodes carinatus*																								
plius of *Balanus*						1																		1
ellaneous				*		†	‡	§																

*Empty egg cases. †Copepodite of *paracalanus*. ‡Broken empty shell. §Empty shell.

	October, 1952																		
Length in mm.	9	10	11 11·5	12	13	14	15	16	17	18	19	20	21	22	23	24	25	Total	12
No. Examined	10.	44	54	88	84	79	78	47	52	48	38	51	22	20	7	4	12	739	3
No. Feeding	7	25	21	36	45	38	25	17	21	14	17	23	15	11	3	2	4	324	1
Coscinodiscus concinnus																			
C. radiatus																			
C. excentricus																			
C. grani																			
C. lineatus																			
Gyrosigma sp.						1												1	
Green patches			2	6														8	
Peridinium depressum																			
Ptychocylis minor	11	88	15	70	168	83	1	60	52	20	45	4				5		622	
Spionid larvae of polychaetes																			
Veliger larvae of lamellibranchs		7	2	6	9	11	3	10	6	1	5	4	1			5		70	
Mactrid larvae																			
Larvae of *Glycymeris glycymeris*		1										2	5	1			6	15	
,, ,, *Musculus marmoratus*					1				1	1			8	6	1		6	24	
,, ,, *Mactra corallina*						1												1	
,, ,, *Limopsis sp.*																			
,, ,, *Montacuta ferruginosa*			2			4					3					1		10	
,, ,, *Spisula elliptica*					1	2		4					1			3		11	
,, ,, *S. subtruncata*				1					2		3		8	3	1		2	20	
,, ,, *Monia squama*								1			1	3	1	5			1	12	
,, ,, *Heteranomia squamula*				1														1	
,, ,, *Anomia ephippium*							1		4	1								6	
,, ,, *Venus sp.1*									1									1	
,, ,, *Venus sp.2*																			
,, ,, *Modiolus modiolus*																			
,, ,, *Cari fervensis*		1		1								1						3	
,, ,, *Astarta sp.*			4	5	1		1					1						12	
,, ,, *Adula simpsoni*			1			3		1		1	1							7	
,, ,, *Tellina pygmaea*			2	5	2	5	1	2	3	2	5		2		1	6	3	39	
,, ,, *T. fabula*							1				1	1	1		1			5	
,, ,, *Ensis siliqua*				2		4			2		3			1				12	
,, ,, *Lima sp.*								1										1	
,, ,, *Hiatella arctica*					1				2	4	9	2	3	4	3	8	8	44	
,, ,, *Cardium sp.*							1									2		3	
,, ,, *Cardium ovale*								1	4	3	8					3		19	
,, ,, *Teredo sp.*																2		2	
,, ,, *Cultellus pellucidus*							2		1		1	1		1	1	1	2	10	
,, ,, *Lepton squamosum*																2		2	
,, ,, *Abra prismatica*			1					1			3	1	2					8	
,, ,, *Mya truncata*							1					1						2	
,, ,, *Aloidis gibba*							1			1								2	
,, ,, *Hiatella gallicana*							2											2	
,, ,, *Mytilus edulis*																			
,, ,, *Montacuta substriata*																			
,, ,, *Zirfaea sp.*																			
Unidentified lamellibranch larvae						2	1	1		1	3		17	3				28	
Lamellibranch eggs					1					1								2	
Gastropod eggs	2																	2	
Limacina retroversa	17	93	59	140	286	266	127	63	85	85	67	117	70	26	27	44	10	1582	1
Copepod eggs	3	10	8	17	13	18	9	7	13	4	6	4	1	2		6		121	
Nauplius of *Calanus*						4			2									6	
Copepodite of *Calanus*																			
Nauplius of *Pseudocalanus*		1	2	4	5	4	1	5	12		8	6	1			14		63	
Copepodite of ,,			1	1	4	5	2	7	2	4	7	2	2	4	2	4		47	
Adult ,,			1	1	2	3	4	3	2	3	3	7	4	3	4		2	42	
Nauplius of *Paracalanus*		2	2	1	5	4	2	1		2	2	3						23	1
,, ,, *Microcalanus*	1			1	2			2			1					10		17	
,, ,, *Metridia*				1			1	1			1							4	
,, ,, *Acartia*	1			1	3	7	4	1	14	6	2	2				4		45	
Copepodite of *Acartia*																			
Nauplius of *Centropages*																			
Copepodite of ,,																			
Nauplius of *Temora*		3	3	7	7	5		5	2	2		1						35	
Copepodite of *Temora*				1						1								2	
Nauplius of *Oithona*	1	1		2	2	1		1	2	4	3			2		8		27	
Copepodite of *Oithona*		2	8	14	17	4	13	24	26	28	22	36	14	52	3	15	3	281	
Adult of ,,		1	2	2	2	5	4				2	1		9	3			31	
Eggs of ,,		8	2	1	3	5	14				2			3				38	
Nauplius of *Microsetella norvegica*			2		2	1							3					8	
Copepodite of ,, ,,				3	1	1		2	2		13	3						25	
Adult ,, ,,	1	1	1	4	5	4	9	5	4	5	3	8	1	2				53	
,, *M. rosea*						2				1				1				4	
,, *Euterpina acutifrons*												1						1	
,, *Halithalestris sp.*																			
Unidentified broken Copepods	1	3	7	5	6	6	3	2	1									34	
Amphipodite of *Monoculodes carinatus*																			
Nauplius of *Balanus*																			
Miscellaneous												*						12	

*12 *Euterpina* eggs

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15	16	17	18 18·5	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	Total
20	18	25	20	20	21	17	15	18	27	18	7	17	12	10	15	2	4	3	2	322
15	6	11	9	11	9	3	9	9	12	6	1	5	2	3	2	0	0	0	0	124
		24				6			2											32
		1																		1
1	5		2		4	2	1		10											29
							1													1
			7				2		10	1										20
					1							1								
												1								1
		1						1												2
1		1	1				1													4
			1																	
						1		1												2
			1																	1
		1						7												8
5		2	4	1	1			7												20
						2			4				5							11
						1							4							5
			1																	1
		2	2	2	1	1	1	1	1						1					12
18	6	13	4		3		1		1											46
1				1	2	1			7											12
													4							4
					1															1
																				1
									1											
		1																		1
	3																			3
									1											1
1			4				2													7
13	12	20	26	17	15	10	16	21	89	60		24	15	13	6					333
4		1	7	1	5	1						1								28
2					5	2	2			1										12
1			4	2	7		1		6											24
8		13	7	10	10	7	7	2	7	5		7	1	2	2					92
3		7	6	3	3	1	2													33
1																				1
										1										1
1																				1
						2									1					3
17	2	12	17	23	25	10	8	4	11	58	10	21		9	1					239
3		2	1	3	5	1			6	6		4		4						38
						6		10												18
1																				4
1			1						3			2								7
7	7	9	5	2	1	2	3													40
								1												1
	2	1		4				1												8

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